The evolution of the hindgut of the deep-sea protobranch bivalves

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Abstract. The evolution of the hindgut of the deep-sea Protobranchia is considered in relation to their feeding strategy. One of the cornerstones of their success in colonizing soft abyssal sediments lies in their ability to digest organic materials extracellularly in relatively low concentration. The time needed to digest such materials contained in a continuous column of sediment in the hindgut is maximized by a much elongated gut. Elongation has been accompanied by a variety of configurations in its course, these maximize the length of the tube that can be housed withih the space of the visceral mass. It would appear that this has been a major evolutionary concern, if not the major evolutionary concern, of the deep-sea protobranchs and has proved to be of considerable taxonomic important.

The Palaeotaxodonta, which comprise the vast majority of the deep-sea (>500m) protobranchs, are all deposit feeders and commonly as many as fourteen species can be collected at a single station both on the lower slope and the abyssal plain (unpub. data). Analysis of the gut contents of specimens representing various species from a single station indicates that all are consuming a similar fraction of the soft sediments. Most, if not all, feed via their palp proboscides in the surface layers of the abyssal sediments and, probably for the most part, on the surface layer itself. In such a situation it is natural to speculate what, if anything, separates the ecological niches of the cohabiting species. In terms of Hutchinsonian Ecology, Allen (1985) has suggested that habit and space could be the separating factors. A more extreme view would be that there is no niche separation, that competition is low and that speciation is neither driven nor restricted by stress. For instance, high pressure could be considered stressful, however having become adapted, in reality all physical factors of deep-sea basins are stable and predictable over geologic time and despite being extreme are unlikely to be stressful. Animal density is low and there is circumstantial evidence that predation is remarkably low (Oliver and Allen, 1980; Turekian *et al.*, 1975), but this may or may not be an indication of the level of competition. Diversity is high however measured (Sanders and Hessler, 1969) with a range of frequency of occurrence of species from common to rare. Community structure in the deep sea is not atypical compared with other marine communities. Apart from indications from morphology of small variations in habit and function (i.e. some species may be less mobile and deeper burrowing than others) it must be concluded that we are as yet largely blind to the delineation of niche for the infaunal protobranchs of the deep sea.

THE PROTOBRANCH GUT

There is one morphological variation that is particularly obvious in the Palaeotaxodonta, namely the configuration of the hindgut. In naive terms it could be concluded that in their evolution the main thrust has been how best to accommodate an elongate hindgut within a small body space rather than changes in external shell morphology to gain ecological advantage in a monotonous environment. External morphological variations are subtle, often to the extent that one taxon can be barely recognized from another (Allen and Hannah, 1986).

Numerically the protobranchs dominate the particulate feeding abyssal bivalve fauna (Clarke, 1962; Sanders *et al.*, 1965). (Note: Carnivorous septibranchs are well represented in the deep sea.) One thing, possibly the only one, that explains this dominance is a difference in the digestive physiology of the protobranchs as compared with the lamellibranchs. Little is known of the digestive processes in protobranchs but what is would indicate a major difference in the function of the digestive diverticula (Owen, 1956, 1980; pers. obs.) as compared with that of lamellibranchs. In the organically rich sediments and water column of shelf seas this difference could be of little significance, but in the relatively impoverished sediments and water column of the abyss (Gage and Taylor, 1991), digestive efficiency is vitally important. The efficiency of the selective process to extract scarce organics within a slurry of fine sediment, together with the time taken to digest skeletal proteins also becomes important.

To maximize extracellular digestion of refractive food material in relatively low concentrations in fine sediments, and the material attached to silt particles, requires an

increased residence time within the gut. An elongated hindgut allows for greater passage time of sediment and a larger surface of contact between digestive epithelium and gut content, allowing for a more complete digestive and adsorptive process. The elongate gut has to accommodate in a small and confined space and this has been accomplished in a variety of ways. Also, an efficient method of transporting a very long column of sediment through a narrow pipe had to be achieved.

To address the last point first, movement through the gut of protobranchs could be dependent, at least in part, on the use of the stomach and the style sac as a squeezable bulb, the pressure so created driving the fluidized gut contents. This is in contrast to the lamellibranchs in which ciliary transport appears to be the driving force. Anatomical observations indicate that pressure can be exerted in two ways. One is via the surrounding musculature basal to the stomach epithelium and the second is via modified anterior pedal retractors, which cradle the ventral side of the stomach (unpub. data). When contracted the latter squeeze the dorsal side of the stomach against the inner shell below the umbo. In the protobranchs the dorsal surface of the stomach lies immediately adjacent to the epithelium of the body wall that lines the shell.

THE HINDGUT OF THE NUCULANOIDEA

The basic design of the hindgut of the nuculanoideans, the most common of the deep-sea protobranchs, is a loop on the right side of the visceral mass (Fig. 1a). The loop extends from the ventral limit of the style sac dorsally posterior to the style sac and stomach, and thence on the right side in a sweeping antero-ventral curve to the mouth and anterior adductor muscle and from there dorsally and posteriorly along the dorsal side of the viscera, passing through the heart and dorsal to the kidney and posterior adductor muscle to the anus. In most species a single typhlosole is present along the whole length of the hindgut.

From this simple configuration a limited number of different types of more complex configurations can be derived. The range of types of configuration is present in a number of families or subfamilies and these types could have evolved more than once in the history of the group.

Although there are exceptions, in general protobranch species with more elongate hindguts are found deeper in the ocean than those with short hindguts. For example, *Tindaria callistiformis* Verrill and Bush, 1897, from depths between 3305 and 5042m, has a hindgut volume per unit animal that is half as large again as *T. hessleri* Sanders and Allen, 1977, from depths between 1739 and 2339m (Sanders and Allen, 1977). More recent measurements of length show that this applies to other protobranch genera, thus *Yoldiella subcircularis* Odhner, 1960, from 3250-5987m, has a hindgut that is more than four times the length of *Y. inconspicua* Verrill and Bush, 1898, from 1102-4829m, in animals of the same size (pers. obs.). The protobranchs are not alone in showing this phenomenon, thus similar increases in gut length with depth were shown in the case of a series of species of the tellinoidean genus *Abra* living at increasing depths (Allen and Sanders, 1966). In many species it would appear that the extended single loop simply takes a wider course around the right side of the body. The diameter of the lumen of the hindgut may also be increased. As seen in the tindariids (Sanders and Allen, 1977) the lengthening of the single loop at its most extreme involves the penetration of the visceral tissue containing the ventral portion of the loop into the mantle of the right side to lie close to the inner muscular fold of the mantle edge. (Fig. 1B). In less extreme cases the ventral limit of the loop lies at the margin of a visceral fold that in large part overlies the right palp. In most cases the lengthened hindgut also penetrates deep into the foot ventral to, and in some cases, anterior to the pedal ganglia. The configuration of the path taken and the diameter of the gut is quite specific and in very many cases the identification of the species can be accurately based on this one feature.

In the progression from a single loop, one sequence involves the coiling of the loop on the right side. This process can be easily illustrated by manipulating a length of rope and taking hold of the anterior limit of a loop and coiling once, twice and eventually more times in a clockwise direction. Individual species have their own characteristic form and number of coils (Figs. 2A-F). Multiple coils have sufficient volume to cause displacement of the stomach to the left, and to limit the digestive diverticulum of the right side to the centre of the coil (Allen and Hannah, 1989).

The second sequence from a single loop is but a variation of that described above. Here the anterior section of the loop extends to the left side of the body passing between the oesophagus and the anterior adductor muscle. On the left side of the body a loop is formed and this, depending on the species, may or may not be coiled in the manner described above (Figs. 2G, H). The morphological consequence of this penetration to the left side of the viscera is to displace the mouth posteriorly. This latter form of hindgut configuration is confined to relatively few species.

Much more common is a third sequence in which the hindgut on reaching the dorsal margin of the visceral mass to the stomach passes first to the left side of the body, makes a loop around the periphery of the visceral mass, then passes to the right side of the body and describes a single loop of similar extent to that on the left (Fig. 3A). Various extensions and modifications to this left and right looped configuration occur in different species. The most common is where right and left loops are doubled on each side. In rarer cases additional loops can be formed on either side. In species with a vertically elongate foot, lengths of gut can be doubled or quadrupled parallel to the style sac and reach far ventral within the foot (Figs. 3B, C).

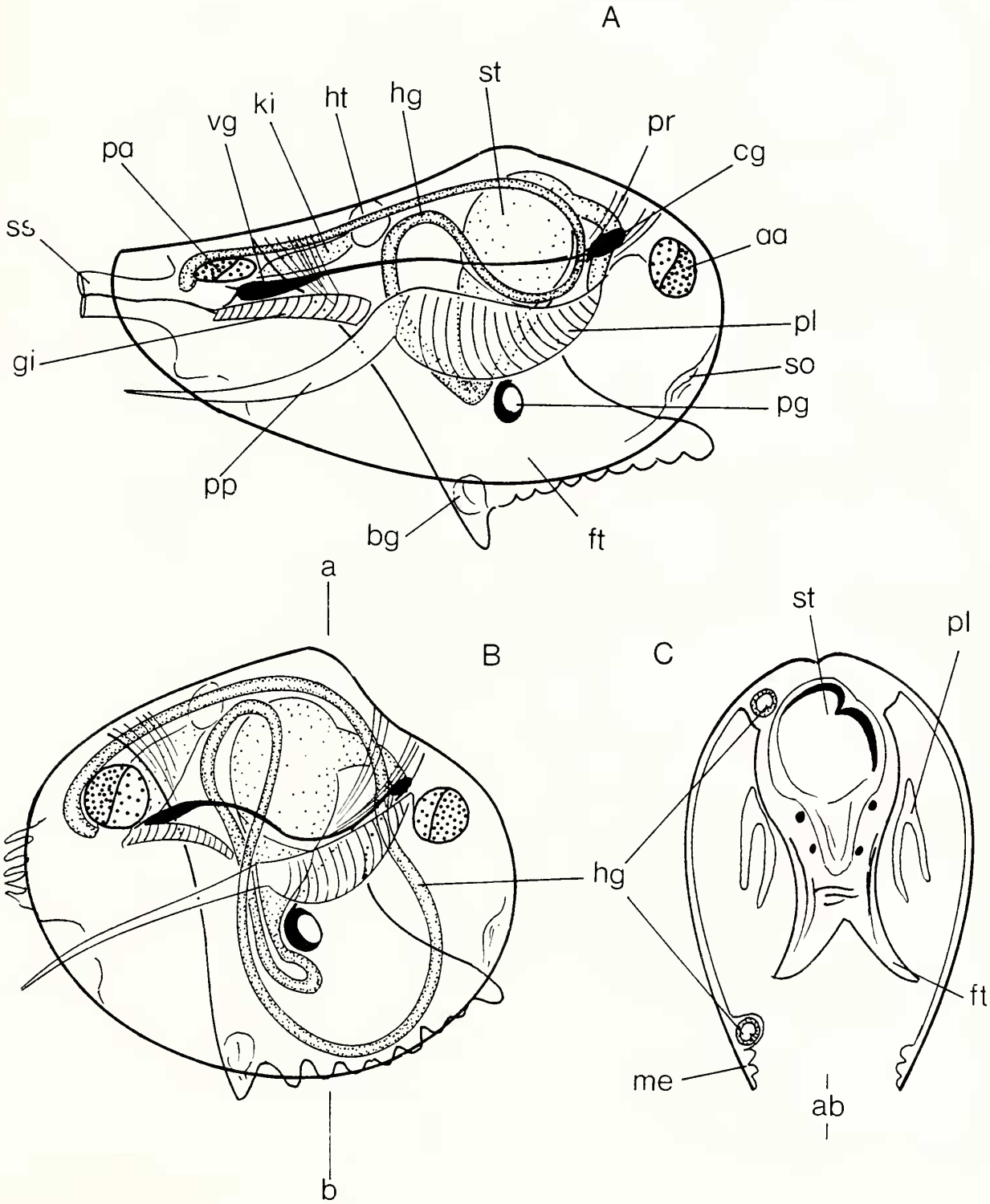

Fig. 1. A, A diagrammatic representation of a generalized nuculanid protobranch from the right side to show the major morphology of the body organs; **B,** a similar diagrammatic representation of a tindariid protobranch as seen from the right side (for identification of the organs see (A); **C,** a diagrammatic representation of a vertical cross-section of a tindariid protobranch through the lines a-b in (B) to show the position of the hindgut. aa, anterior adductor muscle; bg, byssal gland; cg, cerebral ganglion; ft, foot; gi, gill; hg, hindgut; ht, heart; ki, kidney; me, mantle edge; pa, posterior adductor muscle; pg, pedal ganglion; pl, palp; pp, palp proboscides; pr, pedal retractor muscle; so, anterior sense organ; ss, siphons; st, stomach; vg, visceral ganglion.

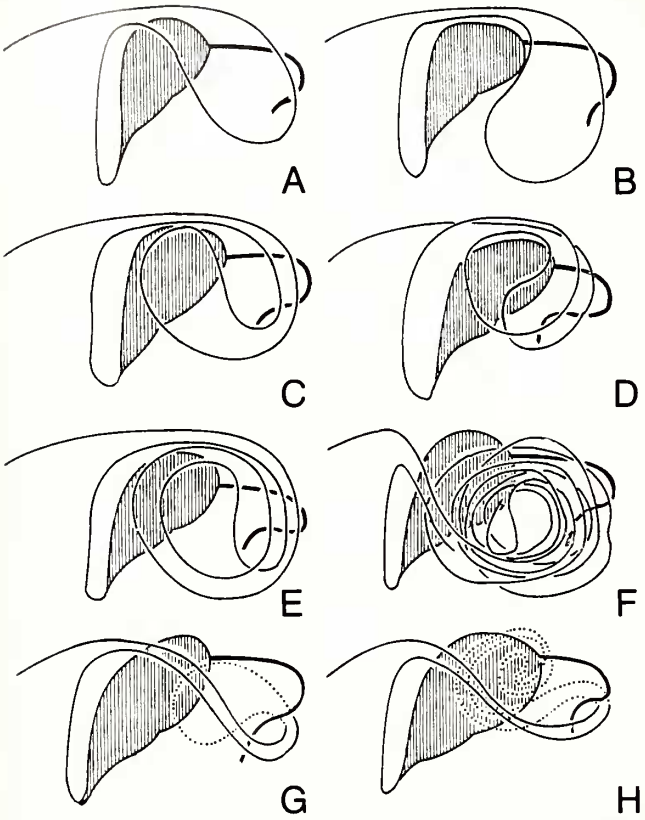

Fig. 2. Line drawings of the course of the gut in eight species of *Yoldiella* to illustrate the different courses taken by the hindgut with increasing length of the hindgut. The drawings are from the right side, the end of the line to the left represents the anus; the end of the curved line to the right, the mouth; the stomach is shown as a 'pear'-shaped outline. The course of the hindgut is shown as a solid line on the right side of the body and as a dotted line on the left.

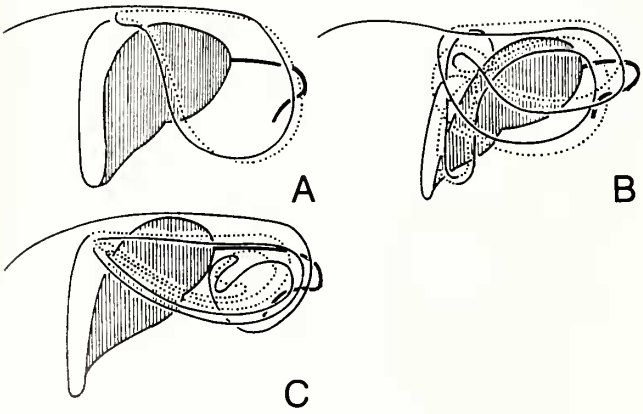

Fig. 3. Line drawings of the different courses taken by the hindgut of three species of *Yoldiella* in which the hindgut loops to both the left and right of the body. The course on the left side is differentiated by a dotted line. Note in all these species the point of passing from left to right and from right to left is posterior to the postero-dorsal limit of the stomach.

In all of the configurations of the second and third sequences described above, the passage of the hindgut from one side of the body to the other occurs either anteriorly between oesophagus and anterior adductor muscle or mid-dorsally immediately posterior to the stomach. It can be pictured that, as the hindgut develops, it is these two points that provide the gateway to the extension to the left side of the body. It is of note that in no species as yet seen does penetration to the left occur at *both* points in an individual species.

In relatively few species penetration of the hindgut to the left side of the body occurs both postero-dorsal to the stomach and *anterior* to the stomach (but posterior to the oesophagus) within the mass of the viscera. As in the second and third sequences this has occurred in well-separated taxonomic groups (Lametilidae and Yoldiellinae) (Allen and Sanders, 1973, unpub. data).

THE HINDGUT OF THE NUCULOIDEA

In the case of the Nuculoideans, no species has yet been described in which there is a hindgut that describes a single loop to the right. Nevertheless, there is much conformity within the Nuculoidean taxa. Thus, the Nuculidae all have a coiled hindgut predominantly dorsal and inclined to the right of the stomach, while the Pristiglomidae have multiple loops to the right and the left passing from side to side postero-dorsal to the stomach but with loops carried dorsal to the stomach and viscera (Sanders and Allen, 1978; Rhind and Allen, 1992).

DISCUSSION

The disposition of the hindgut provides additional clear evidence of the differentiation of the Nuculoida into the Nuculoidea and Nuculanoidea - already well-established on other morphological and functional grounds (e.g. the presence or absence of an anterior inhalent current, anterior mantle sense organ and posterior inhalent and feeding apertures) (Fig. 4). Hindgut differences clearly differentiate the two nuculoidean families, the Nuculidae and the Pristiglomidae.

Similar universal differences cannot be seen in the case of the nuculanoideans. In a few families there is a predominant hindgut configuration (Fig. 4). These more clear-cut examples include the Nuculaninae, which possess a single loop to the right that is not particularly lengthened, and the Malletiidae and the Tindariidae in which the single loop is extended (Sanders and Allen, 1977, 1985). In the latter family the hindgut is usually carried into the right mantle lobe. In the Spinulinae, multiple coils are present on the right side of the body in most species (Allen and Sanders, 1982). In contrast, species of the Ledellinae (Allen and Hannah, 1989), the Yoldiellinae and the Neilonellidae (unpub. data) exhibit a wide range of configurations. Whether or not these groups

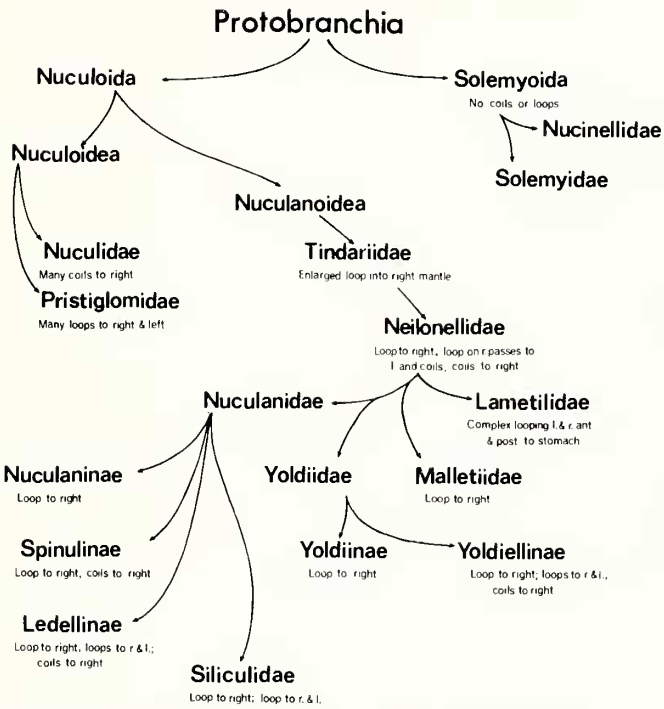

Fig. 4. Possible evolutionary relationships within the Protobranchia.

are discrete entities or whether they are polyphyletic is not yet absolutely certain. In the case of the Ledellinae, the subfamily comprises a series of closely related species in which other characters, particularly those of the shell, show not only close relationship but are sufficiently distinct as to delineate a suprageneric taxon. This is less clear in the Yoldiellinae (unpub. data), which comprises a very large number of species, but without the strongly marked shell characters displayed by the Spinulinae and Ledellinae. Overall the differences in shell characters are so slight as to be impossible to arrange the species into distinct units. The Neilonellidae are presently under review, but the indications are that this family exhibiting a variety of gut configurations is monophyletic (pers. obs.).

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